Foraging specialisms influence space use and movement patterns of the European eel *Anguilla anguilla*.

Final version accepted by Hydrobiologia

J. Barry[1], M. Newton[1], J.A. Dodd[1],O.E. Hooker[1] P. Boylan[2], M.C Lucas[3]AND C. E. Adams[1].

1. Scottish Centre for Ecology & the Natural Environment, IBAHCM, University of Glasgow, Rowardennan, Glasgow, G63 0AW UK.

2. Loughs Agency, 22 Victoria Road, Derry, Northern Ireland, BT47 2AB, UK

3. School of Biological and Biomedical Sciences, Durham University, South Road, Durham DH1 3LE, UK.

Corresponding author:
jbarry16@gmail.com
00353861761817

Abstract

A fixed receiver array was used to examine the movement patterns and space use of the European eel *Anguilla anguilla* in an oligotrophic Irish lake between July and September. We assessed home range size, temporal change in spatial behaviour and activity patterns of broad headed (n=11) and narrow headed (n=8) morphotypes. Broad-headed individuals displayed a larger home range (mean KUD_{95} (km^2):0.296 ± 0.04 S.E.) in comparison to narrow-headed individuals (mean KUD_{95} (km^2):0.143± 0.02 S.E.). Eel activity was strongly dependent on light conditions. Narrow-headed individuals' movement peaks occurred at dawn and dusk in comparison to broad-headed individuals which exhibited a more stable movement pattern throughout night and into dawn, suggesting that narrow-headed eels are more crepuscular in nature whereas broad-headed individuals are more nocturnal. Lunar phase period also influenced eel movement within the lake. These results provide valuable insights into the spatio-temporal distribution of yellow eels in a lake system, demonstrating that individuality in foraging behaviour has direct influence on spatial patterns.

Keywords: Anguillidae, Home range, foraging specialisms, morph, diel patterns

Introduction

Understanding how animals utilise their habitat in both space and time provide insights into the ecological, competitive and environmental forces that shape their behaviour. Increasingly, telemetry is used to quantify spatial (e.g. home range) and temporal (e.g. diel phase) activity patterns to evaluate individual distribution (Lucas & Baras, 2001; Cooke et al., 2012). These patterns encapsulate movement behaviours associated with fulfilling ecological needs (feeding, shelter etc.) and are regulated by predictable variation in the environment. Home range is an area over which an animal regularly travels (Burt, 1943; Powell & Mitchell 2012). A home range is considered to be a decision-making process shaped by natural selection, increasing the contribution of resources to fitness, which are spatially distributed in a habitat (Mitchell and Powell 2004). Thus home range represents interplay between the environment and an animal's understanding of that environment (Borger et al. 2008; Powell 2000).

Fish body size, and thus energetic demands, can markedly influence home range size (Jetz et al., 2004; Killen et al., 2007). Increased home range of larger individuals is associated with a behavioural response to optimise foraging for the elevated energy demands (Dahlgren & Eggleston 2000; Marshall et al., 2011). Home range size and activity patterns can also be dependent on diet and the foraging tactic employed, for example carnivores typically occupy larger home ranges than herbivores (Peters, 1986).

An important driver of fish distribution is that of feeding opportunity, with fish responding to resource type and or availability within a given habitat (Clark & Levy 1988; Jackson et al., 2011). Individual specialisation in diet is relatively common among wild populations of many species (Bolnick et al., 2003). Individual feeding specialisations can be temporally stable and associated with the occurrence of discrete morphotypes (Skulason & Smith 1995). Such foraging specialisms seem to be particularly common in fishes found in post-glacial lakes (Garduno-Paz et al., 2010; Siwertsson et al., 2013). Interspecific differences in head morphology of fish are known to reflect differences in feeding behaviour (Adams et al., 1998, Kristjansson et al., 2002) and are generally a result of consistent individual differences in foraging and diet over time.

The European eel (*Anguilla anguilla* L.) occupies a wide range of aquatic systems and habitat types, including fresh, brackish and salt water (Moriarty & Dekker, 1997). If drainage basins have natural or artificial lakes with adequate passage for migrating juveniles and adults, they will represent important growth habitat (Laffaille et al., 2004) producing high numbers of silver eels (Tesch, 2003). Determining space use by eels in lake systems is thus important for an understanding of their ecology and ultimately conservation management in such systems. The existence of foraging specialisms amongst individuals of eel in freshwater populations is reasonably well known (Lammens & Visser, 1989; Ide et al., 2011) and such specialisms seem to be associated with the dichotomous description of "broad-headed" and "narrow-headed" individuals (Lammens & Visser, 1989; Proman & Reynolds, 2000; Ide et al., 2011). These studies have shown that independent of body length, broad-headed specimens tend to be piscivorous and narrow-headed individuals feed predominately on benthic invertebrates with this discrete variation among individuals being evident in the same locality (Cucherousset et al., 2011; Ide et al., 2011). However, the extent to which the observed morphological variation is associated with behavioural differences other than those linked with feeding is yet to be investigated.

Information about how they utilise lacustrine habitat is essential to help direct conservation strategies. Despite the length of time eel spend in lacustrine environments, there is little information about home range size and activity patterns in lakes. The first objective of this study was to quantify the spatial distribution of European eel, with a specific focus on home range sizes and activity patterns in a lacustrine habitat. Combining measures of individual head morphology with individual behavioural parameters obtained by tracking movements of individuals using acoustic telemetry, our second objective was to test the hypothesis that individual movement patterns and space use are correlated with differences in morphology and foraging specialisms.

Methods

STUDY AREA & RECEIVER ARRAY

Lough Finn is an oligotrophic freshwater lake located adjacent to Fintown, Co. Donegal, Republic of Ireland (54 ° 51.7 N ' 008 ° 8.04' W). The lake is entirely natural, there are no obstructions in vicinity of the outflow so that eel are free to enter and leave the lake. Other fish species present in Lough Finn are, brown trout (*Salmo trutta*), Arctic char (*Salvelinus alpinus*) and Atlantic salmon (*Salmo salar*), with no introduced species present. Lough Finn is approximately 1.15km^2 (115 ha) in size with a mean depth of 11.5m and a maximum depth of 21m. An echosounder linked to a GPS was used to record depths across a series of intersecting transects and these data were used to create a bathymetric map using Arcview GIS.

Preliminary tests were undertaken to determine the detection range of acoustic tags and receivers in Lough Finn. Based upon these preliminary detection range estimates, a fixed array of 20 omnidirectional acoustic receivers (69 KHz, Vemco VR2W) was deployed throughout the lake (Fig. 1). Receivers were attached (3 m from the bottom) to a rope riser on a moored anchor system, in 10-15 m depth of water. The receiver configuration allowed for range overlap (see below) and thus allowed tagged fish, that remained in the lake, to be continuously detected throughout the study.

FISH SAMPLING AND TAGGING

Yellow eels were captured using fyke nets on 27 June 2013 and again on 2 July 2013. Nets were set arbitrarily around the lake and fished for a period of 24 h. Each fish was classified using the silvering index of Durif et al. (2005) so as to ensure all individuals tagged were resident and in the growth phase of their life cycle. Individuals in stage I-III were considered suitable for tagging and individuals which were categorised as stage FIV and FV were rejected from the study due to the high possibility of them metamorphosing and beginning downstream spawning migration in the near future. Overall, twenty individuals were tagged with individually coded 69KHz acoustic transmitters (Model LP-7.3, 7.3mm diameter, 18mm length, 1.9g weight in air, 139dB re 1 µPa power, Thelma Biotel AS, Trondheim, Norway 2013). Acoustic transmitters were programmed to each have an average acoustic transmission repeat cycle of 120s. The mean total length and mass of tagged fish was 498± 91.3mm and 227±141.1g (range: 390-720mm, 90.3-602g). The mean tag to body mass ratio was 1.11±0.5% (i.e. <2% as recommended, *sensu* Lucas & Baras, 2000). For the tagging procedure, fish were anesthetized by immersion in a water clove oil solution (0.5mg per litre) until loss of equilibrium. Fish were placed in a v-shaped support and an acoustic transmitter was surgically implanted through a 15mm incision into the peritoneal cavity, and the incision was closed with independent sterile sutures (6-0 ETHILON, Ethicon Ltd, Livingston, UK). Fish were aspirated with 100% lake water throughout the procedure. The entire surgical process took less than 4 minutes. After complete recovery, defined as correct orientation and response to stimuli, fish were released in the location of initial capture. Recent work has demonstrated that this surgical procedure does not adversely affect behaviour of eels (Thorstad et al., 2013).

DATA ANALYSIS

Head shape analysis

Where possible, an equal number of fish from broad and narrow-headed morphs were selected (*sensu* Proman & Reynolds 2000). Overall, twelve broad-headed individuals and eight narrow-headed individuals were tagged with individually coded acoustic transmitters. For each individual fish, head width (HW, to the nearest 0.1 mm) was measured between the outside of the jaw hinges, along with total body length (TL), the ratio HW:TL was calculated for each individual at tagging and subsequently used to assign tagged individuals to either broad (>0.33) or narrow (<0.33) according with previous studies (Lammens & Visser 1989; Proman & Reynolds 2000). To verify that this was an appropriate indicator of head shape we used a model-based clustering approach implemented in the package MCLUST for R (Fraley & Raftery 2009). Lateral view photographs of all fish were taken using a Cannon EOS 350D digital camera for geometric morphometric analysis. For each photograph a reference scale was included to allow the removal of shape change associated with size. Before comparing head shape of the groups a pooled within-group regression of Procrustes co-ordinates on log centroid size was performed. The residuals from this were derived thus providing a measure free from allometric scaling of shape associated with size (Klingenberg, 1998). Nine consistently identifiable landmarks were digitised in two dimensions (Fig.2). Land marks were carefully chosen to represent overall head shape. Principle component analysis was undertaken on Procrustes coordinates (2D coordinates that have been standardised for size and position) of the nine landmarks used to describe head shape. Principle component scores for each individual fish were clustered to allow an objective examination of head shape and assignment to ecological sub-group with clustering software. Two MCLUST models (EII and VII; see Fraley & Rafety 2006 for model descriptors) were fitted to the first four principal component scores of head shape data. The “best” models, representing the most likely number of groups on the basis of head shape, were identified using Bayesian Information Criterion (BIC). The BIC value is the maximised log-liklihood for the model, the data dimensions and the number of model components; the larger BIC, the stronger the support for the model for head shape. The model that could at a minimum discriminate broad and narrow headed eels and had the highest BIC was selected to test accuracy of field classification method. For tagged fish, comparison between the best model with the next best model (resulting in a different number of groups) was undertaken by calculating ΔBIC as the difference in the BIC-values between the best model and the next best model. Following Kass

& Raftery (1995) interpretation; ΔBIC>10 as very strong support, 6<ΔBIC<10 as strong support, 2<ΔBIC<6 as moderate support, and ΔBIC<2 as equivalent support for the best and the next best model. Statistical analyses were conducted in the R statistical computing package (R Development Core Team, 2014).

Acoustic position estimates

We estimated centres of activity (COA) for each fish for an allocated time bin using the mean position algorithm described by Simfendorfer et al. (2002). R statistical computing language R development Core team (2014) was used to calculate mean latitude and longitude of all detections within each sequential time interval. The resulting set of estimated positons was used for the subsequent analysis. Fish position at each time was based on the averaged positions of the receivers that detected fish during the time interval and weighted by the number of detections at each receiver (Simpfendorfer et al., 2002; Hedger et al., 2008) to provide an estimated location for that time period. To test the assumption on which the centre of activity mean position algorithm is based; that the number of tag detections decreases with increasing distance from a receiver, a tag detection range test was undertaken. Transmitters (Model LP-7.3, 40-120s delay, 139dB re. 1 μPa, Thelma Biotel AS, Trondheim, Norway 2013) were moored at seven known distances from a receiver for 72 hours, and the number of receptions was determined each day for each distance. There was a significant negative linear relationship between the hourly number of receptions, relative to transmissions, and the distance from a receiver ($r^2 = 0.91$, $P < 0.001$). Thus the assumption of linearity that underlies this methodology was supported for the equipment within Lough Finn. Tag detection ranged from 50m-450m. Based on this range testing of equipment, the maximum distance at which a signal was detected at least 50% of the time was estimated at ~320 m and this distance was therefore used in array design to ensure sufficient detection overlap between receivers. Following Villegas-Rios et al. (2013), to select the optimal time bin we calculated the mean number of receivers detecting signals from an individual tag (NR) and then we averaged the number of detections from this tag across all receivers (ND) during each time bin. The number of receivers (NR) detecting a tag is expected to increase asymptotically as time bin size increases, whereas the number of detections (ND) increases linearly with time bin size. Better position estimates are obtained when the fish is detected multiple times by multiple receivers. A suitable time bin was determined when the increase in NR was <10% between two consecutive values and ND remained >10 (Villegas-Rios et al., 2013). The resulting value was 60 minutes at which mean NR was 2.93 ±0.4 and mean ND was 24.05±

14.2. This ensured adequate spatial resolution of the data while maximising temporal resolution. In order to prevent bias of fish positions due to post tagging effects, all fish positions recorded until 4 days after release were excluded from analysis to allow the fish to recover sufficiently and resume normal movement behaviour.

Home range analysis

To avoid temporal autocorrelation and ensure independence of fish locations, Incremental Area Analysis (IAA) was conducted according to Hodder et al. (2007) to gauge the number of positions needed to represent maximum home range of individuals. From IAA a standardised sample of 108 positions per fish was used to examine monthly home range, this ensured a sufficient sample size and temporally stratified distributions of fish locations. Positions in the sample were chosen arbitrarily to represent the correct proportion of the number of hours in each time of day category (dawn, day, dusk, night; based on the NOAA sunrise/sunset calculator (NOAA, 2014) during each month.

Kernel Utilisation Distribution (KUD) was used as a home range estimator for eels. KUD estimates the intensity of area use of an animal's location over time (Worton, 1989). An animal's relative frequency of occurrence in a two-dimension plane was based on stratified locations throughout the study. To create 50% (core area) and 95% (home range) kernel estimates Geospatial Modelling Environment (GME) was used in conjunction with ArcGIS (v.10.1), KDE and isopleth tools were used to create 50% and 95% kernel distributions (KUD_{50} & KUD_{95}) for each individual fish in GME (Bandwith = LSCV, cellsize=50m). Area calculations (km^2) of 50% and 95% kernel estimates were undertaken in ArcGIS. These polygons (containing 50% and 95% kernel estimates) were then clipped to the lake polygon (using the Intersection tool in ArcGIS) to exclude any portion of the calculated home range that occurred on land. To determine whether the location of monthly space use changed through time, the proportion of overlap between 50% and 95 % KUDs from month to month was calculated using the ArcGIS. Overlap was represented as the proportion (%) of the previous month's value and represented changes in month-to-month activity space. Finally depth preference was investigated for eels by employing the zonal statistics tool (ArcGIS) to obtain mean depth occupancy in KUD_{50} assuming eels maintain a benthic lifestyle within their core range.

To investigate differences in home range size (KUD_{50} and KUD_{95}) between morph type and month, a linear mixed effect model (LME) was constructed. A LME was also constructed to investigate the effects of mean water temperature and duration of night (minutes) on mean monthly KUD size between morphs. In all LMEs “individual” was treated as a random factor to account for repeated measures. Linear models were used to investigate; the effects of eel length and weight on mean KUD size; to test for differences in space use overlap (KUD_{95} & KUD_{50}) for both morphs and; to investigate the influence of fish length and temperature on depth preference in (KUD_{50}). Differences in depth use in the core area (KUD_{50}) between morphs were compared using Welch's t-test. KUD data and KUD overlap data were transformed (log and arcsine transformed respectively) prior to analysis to improve normality. All model diagnostics were assessed graphically by examining the residuals for heterogeneity. For LME’s *P* values were generated for fixed effects using the log likelihood method, by comparing models with and without the term(s) in question. All analysis was conducted using the R statistical computing package.

Movement patterns

The aim of the modelling process was to determine what factors were influencing eel movement within the array. Minimum displacement rates were obtained by calculating straight line distance between consecutive COA’s (centre of activity), converted to body lengths / hour (BLh^{-1}) to standardise for body length effect. Linear mixed effect models were used with a random intercept following Zuur et al. (2009) and Pinheiro & Bates (2000). Including fish ID as a random effect, the model accounted for potential correlation between repeated measures on each individual. Independent variables were interrogated for colinearity and variance inflation scores were used to verify variable suitability. A second LME was used to test the effects of average displacement rates per hour per month for individuals (continuous response variable) and fixed effects included; the individual’s physical characteristics (length and head shape), month and hour of day. A third LME was constructed using average daily displacement (m) rates as the response variable with water temperature, duration of night and lunar phase as fixed effects. The lunar cycle was categorised into eight phases: new moon, waxing crescent, 1st quarter, waxing gibbous, full, waning gibbous, 3rd quarter, waning crescent based on the percent of the moon illuminated using R package “lunar” (Lazaridis, 2015). Duration of night was measured in minutes of darkness based on NOAA calculator (NOAA, 2014).

In both LME's the glmulti function, with a wrapper to enable use of a random effect (Calcagno & Mazancourt 2010) was used to allow model selection of the best set of independent variables up to two way interactions with minimum Akaike information criterion (AIC). For both LME's final models were generated with non-significant variables dropped. Model diagnostics were assessed graphically by examining the residuals for heterogeneity. *P* values were generated for interactions and fixed effects using the log likelihood method, by comparing models with and without the term(s) in question. All analysis was conducted using R statistical computing package.

To examine the potential effects of the five fish which left the system (potentially as silver eels) and the potential for behavioural differences during the period they were tracked data analysis was performed excluding these fish in all tests. Excluding these five fish from the analysis did not change general trends or change statistical significance in any cases.

Results

FISH DETAILS

In total 20 (12-broad-headed, eight narrow-headed) European eel were individually tagged and tracked during this study (Table. 1). On average, an individual fish was detected on 12.2 ± 0.76 receivers over the study period. The detection period for tagged fish ranged from 44-95 days (Table 1). Five of the 20 eels (broad headed individuals: 2315, 2329, 2335 and narrow head individuals: 2334, 2322) left the array within the lake system and where last detected at the receiver nearest to outflow stream. One broad headed individual (2318) exhibited behavioural movements between river and lake system and was removed from analysis due to the bias of this fish on home range estimates, The number of eels used in analysis per morph per month is presented in Table S1 (supplementary information).

MORPH CLASSIFICATION

A model containing the first four principal components from an ordination of geometric head shape was used to discriminate head shape group of tagged fish. Based on BIC scores the MCLUST model EII (Fraley & Rafety 2006) supported two clusters (1 group BIC=264.8; 2 groups BIC=304.21, ΔBIC>10 providing support for 2 groups). The assignment of individuals from cluster analysis grouping matched directly with broad and narrow head classification based on HW:TL ratio assignment (*sensu* Proman and Reynolds 2000) thus ensuring adequate morph categorisation (Table 1).

HOME RANGE AREA ESTIMATES

Home range estimates are presented as the average KUD$_{50}$ (core area) and KUD$_{95}$ (home range area) (km^2), per month for both broad-headed and narrow-headed morphs of eels (Tables S1, S2). Over the duration of the study period broad-headed individuals displayed a larger home range (mean KUD$_{95}$:0.296 km^2 ± 0.04 S.E.) in comparison to narrow-headed individuals (mean KUD$_{95}$:0.143 km^2± 0.02 S.E.) (Table 2). KUD$_{50}$ size was not significantly affected by month (χ^2=0.844,df=2, P=0.655) or head shape (χ^2=1.87,df=1, P=0.17). Month did not have a significant effect on KUD$_{95}$ area estimates (χ^2=4.11,df=2, P=0.127) however the model revealed a significant effect of head shape (χ^2=11.169,df=1, P=0.0001) indicating that broad-headed individuals had larger KUD$_{95}$ ranges in comparison to narrow-headed individuals. Mean water temperature per month had a significant positive effect on mean KUD$_{95}$ size for both broad-headed and narrow-headed individuals (χ^2=10.865,df=3, p=0.012) however no effect of temperature was found on mean KUD$_{50}$ (χ^2=0.0996, df=1, P =0.565). Mean duration of night per month (minutes between sunset and sunrise) did not significantly affect KUD $_{50}$ of eels (χ^2=2.40, df=1, P =0.122). However the model revealed a significant interaction between month and morph (χ^2=8.2286, df=3, P =0.04) this was explained by a negative effect of increasing night duration on KUD $_{95}$ size of narrow- headed individuals.

Body length and mass had a positive effect on KUD$_{95}$ of all individuals (Length t=2.486, $_{2,16}$ P<0.05; mass t=3.455, $_{2,16}$ P<0.001). Controlling for length broad-headed individuals had a significantly larger KUD$_{95}$ than narrow-headed (t=4.951, $_{1,15}$, P <0.05) (Fig.3). KUD$_{50}$ size was significantly positively affected by length of individuals (t=3.069 $_{2,16}$, P<0.001) but no differences were observed on KUD$_{50}$ size between morphs when controlling for length (t=-0.349 $_{2,16}$ P>0.05).

The amount of overlap in KUD area from month to month was used to define reuse of space through time as an indication of fidelity to home ranges. Average monthly overlap of 41% and 70% was observed for KUD$_{50}$ and KUD$_{95}$ respectively (Table 3). KUD$_{95}$ overlap between consecutive months was similar in both morphs (Broad=69% Narrow = 70%). Mean overlap between consecutive months of individuals' KUD$_{50}$ was significantly higher in broad-headed individuals (t=2.453, $_{3,15,}$ P <0.05) indicating higher site fidelity in this group. Further analysis revealed a significant interaction between length of individuals and head shape on KUD$_{50}$ overlap between months (t=-2.838, $_{3,15}$, P <0.05) indicating that small size narrow-headed individuals exhibit higher overlap between KUD_{50} compared with large size narrow-headed individuals, this contrasts with broad headed individuals which exhibit consistent overlap between core KUD's regardless of size. Differences in patterns between 50 and 95 % KUDs suggest individuals maintained a consistent KUD_{95} area that was reliably reused through time, but that the extent of movement in KUD $_{50}$ varied in particular among larger narrow -headed individuals resulting in lower degrees of overlap in core area.

The mean depth use of tagged eels at lake bed level in their estimated (KUD_{50}) was 9.0 meters. There was no relationship between mean depth in their KUD_{50} and length of individuals (F=0.384,$_{1,17}$ P = 0.74, r^2 = 0.02). Depth preference did not differ significantly between morphs (Welch t-test: t=-0.216, d.f. = 14.03, P =0.68). No relationship was found between mean depth in core area (KUD_{50}) and water temperature (F=0.224,$_{1,67}$ P = 0.604, r^2 = 0.004) over the duration of the study.

MOVEMENT PATTERNS

Diel movements

The minimal adequate linear mixed model for eel diel movement revealed a significant effect of hour of day on broad-headed (χ^2=21.013,df=1, P <0.001) and narrow headed individuals (χ^2=5.14,df=1, P <0.05) both morphs exhibited a clear nocturnal diel pattern with higher average BLh^{-1} displacement observed during crepuscular and nocturnal periods compared to during daylight (Fig.4). To explore further the relationship between diel patterns and average displacement, hour of day was grouped into light categories based on NOAA calculator (sunrise/sunset calculator (NOAA, 2014). Light category was found to have a significant effect on average hourly displacement BLh^{-1} of tagged fish (F=14.54 $_{3,80}$ P<0.001). The magnitude of effect for was greater for broad-headed eels over duration of study, with broad-headed individuals having higher average hourly displacement rates than narrow-headed individuals (Fig. 5). Broad-headed individuals average displacement rates were significantly higher during night and dawn over other light categories (P<0.05 in all cases) however no significant difference was observed between dawn and night for broad-headed individuals (P>0.05). Narrow-headed individuals had significantly higher average displacement rates during dawn and dusk over other light categories (P<0.05 in all cases) however no significant difference was found between dawn and dusk categories for narrow-headed individuals (Fig.5).

Environmental correlates

The minimal adequate linear mixed model investigating the effects of environmental correlates revealed a significant positive effect of temperature (χ^2=8.16, df=1, *P* =0.004), increasing duration of night did not have a significant effect on broad-headed individuals (χ^2=1.803 df=1, *P* =0.321) and lunar phase was found to have a significant effect (χ^2=19.724, df=1, *P* =0.006) on average daily displacement (Blh^{-1}). Broad-headed individuals' average daily displacement was found to be higher during waxing lunar phases. Narrow-headed eels average daily displacement was not influenced by temperature (χ^2=1.469, df=1, *P* =0.225), increasing duration of night had a significant negative effect on narrow-headed individuals (χ^2=40.803 df=1, *P* =0.001). Lunar cycle had a significant effect (χ^2=18.108, df=7, *P* =0.01) with narrow-headed individuals' average daily displacement peaking on waning lunar phases (Fig.6).

Discussion

There are numerous studies detailing the extent of intra-population variation and individual specialisation in traits as a result of diet and foraging (Bolnick et al., 2003; Araujo et al., 2009). Detailed studies that link together spatial, temporal and individual level processes are however, rare. Here we report that yellow-phase lacustrine European eels exhibit strong correlations between head morphology and spatial behaviour. This study is the first to provide an extensive account of home range size and movement patterns of European eel in a lake system. The lake system in which our study took place allowed for continuous observations of eel movements over the study period. While this study supports previous findings of extensive movement patterns of yellow eels (Thiabult et al. 2007, *A. rostrata*; Walker et al., 2014, *A. anguilla*) we add to the understanding of home range variation and activity presenting evidence of movement patterns being influenced by diurnal and lunar drivers of activity as well as behavioural differences leading to variation in space use.

These findings support current evidence that *Anguilla* species establish a home range while resident during the continental stage of their lifecycle (Parker, 1995; Morrsion & Secor 2003). Studies have documented varying home range sizes for eels in different habitat types. Reported home ranges in small lakes, tidal creeks and estuaries have varied in size 0.0027 km^2 (LeBar et al., 1987), 0.01 km^2 (Bozeman et al., 1985), 0.16 km^2 (Thibault et al., 2007) and 3.25 km^2 (Parker, 1995). Thus, the factors that drive within species variation in space use and home range size remain poorly understood and examples from previous studies suggest they may change depending on habitat type and individual eel characteristics.

Our results suggest that total length and weight of individuals are important predictors of home range size. This finding is consistent with the allometric scaling relationship between body size and space requirements (Jetz et al., 2004). Thiabault et al. (2007) observed an allometric relationship between total length and increased home range for American eels in tidal estuaries, comparable to results in the present study. The relationship between body size and home range size may result from the increased area required to provide the resources for a larger individual (Swihart et al., 1988; Pearce et al., al 2013). Kramer & Chapman (1999) proposed that allometric shifts in change of diet and decreased relative cost of swimming were potential drivers for this observed pattern.

Our findings indicate differences in KUD_{50} and KUD_{95} areas between eels within the lake. A KUD_{50} is an eel's core/high use area whereas KUD_{95} is an eel's maximum range. Head morphology was found to be a significant predictor of eel's maximum range in this study. Our study provides the first empirical evidence that this observed morphological variation in eels leads to significant differences in home range size. Over the entire study period broad-headed individuals were found to have a significantly larger home range than that of narrow-headed individuals. Variation in a space use as a result of different morph type has been observed for other predatory lacustrine fish (Kobler et al., 2009). The increase in home range size could be in part, due to the higher mobility and greater space use requirements of fish prey that are targeted by broad headed individuals in comparison to more localised prey availability of invertebrates for narrow head individuals. In terms of lacustrine eels KUD_{50} core areas can be deemed as resting and or foraging areas and these areas do not differ significantly between broad headed and narrow headed individuals. In comparison to KUD_{95} (maximum range) which may represent foraging excursions or searching for prey which was found to be significantly larger in broad headed individuals and is potentially as a result of the movement of fish prey between larger areas in comparison to invertebrate prey of narrow headed individuals which would be more localised.

Overall home ranges remained stable over the study period for both morphs with monthly comparisons of range shift revealing mean home range overlap for broad-headed of 69% and 70% for narrow headed individuals. The observed home range stability from this study supports findings of site fidelity within eels (Parker 1995 ; Baras et al., 1998; Beguer-Pon et al., 2014). Homing behaviour has been observed for both *A.anguilla* and *A.rostrata* respectively (Tesch, 1967, Lamoth et al. 2000). Tesch (2003) found that burrows and cavities were utilised as resting places and shelter for the eels and studies have documented the fidelity of tagged eels to discrete refuges (Ford & Mercer, 1986; McGovern & McCarthy, 1992). Walker et al. (2014) demonstrated that estuarine eels return to the same site every night which also support the findings of site fidelity from this study. The high level of site fidelity observed among eels may in turn contribute to maintenance of habitat associated phenotypic divergence.

Although KUD_{95} remained relatively stable throughout the study period, significant variation in high-use core areas (KUD_{50}) was observed between different morphs, in terms of continued space use over time. Narrow-headed individuals exhibited a significantly higher core range overlap in comparison to broad headed individuals. We hypothesize that the differences observed in core area space use is a direct result of foraging behaviour. Given the feeding strategy of broad-headed individuals as ambush feeders, they are likely to consume large meals and remain immobile for long periods while digesting (Fu et al., 2009) and may have optimal feeding locations “ambush points” where an encounter with prey fish is high, therefore increasing spatial overlap and thus site fidelity to high use areas. In comparison, lower overlap in core area use by narrow headed individuals may be a direct result of resource availability and the need to move will be higher for insect feeders due to patch depletion (Pyke, 1984).

In this study, mean depth zone occupancy by individual eels in a high intensity area (the most utilised area KUD_{50}) ranged from 1.5m – 22m but averaged 9m, assuming eels adopted a benthic lifestyle. This study could not identify drivers of depth occupancy in eels. Length, morphotype (broad, narrow) and temperature did not significantly affect depth occupancy in the high intensity area of use. Yokouchi et al., (2009) found catches of eels in an Irish lake were lowest from 0.5 – 5m and greatest at the deepest depth range 22.5-25m, Anguillid eels are generally thought to adapt to the environment in which they reside therefore the depth distribution of *A.anguilla* in lakes may depend on the physical and biological characteristics of each lake as well as the occurrence of oxygen-depleted layers which may occur in thermally stratified lakes. Unfortunately, dissolved oxygen data were not available in this study, but since Lough Finn is oligotrophic and a cool climate, it is unlikely that oxygen depletion of deeper waters occurred.

While the European eel is believed to be relatively sedentary while in freshwater (Riley et al., 2011), studies have revealed that eels also can utilise large areas and undertake regular movements in estuarine environments (Hedger et al., 2010; Walker et al., 2014; Beguer-Pon et al., 2015). The substantial levels of movement and clear diel activity patterns found in the study reported here imply active foraging strategies within their stable home ranges. Rosten et al. (2013) found that in spring and summer yellow eel in a southern English chalk stream exited a side channel and returned at dawn, presumably foraging in the main channel by night and using the side channel as daytime refuge habitat. The strong influence of light conditions has been noted in other studies; telemetry studies of American eels in estuaries and salt marshes demonstrated increased activity at night (Helfman et al., 1983, Thiabault et al., 2007, Hedger et al., 2010, Beguer-Pon et al., 2015). European eels have also been found to be more active at night in estuarine environments with the start and end time of movements being strongly associated with sunset and sunrise respectively (Walker et al., 2014). The results from this study further support this pattern of strongly nocturnal and crepuscular activity. Hedger et al. (2010) suggested nocturnal movements to be indicative of fish hiding in the substratum during the day and moving into the water column to forage under the cover of darkness. While our study confirmed that yellow eels are more active at night. Interestingly activity of narrow-headed individuals' decreased with increasing night duration and the resulting shortening of crepuscular periods. This indicates a strong relationship between dawn and dusk periods among tagged narrow-headed individuals.

Lunar phase was also shown to be a significant predictor of eel movement in this study. It has been well documented that there are intrinsic links between eel behaviour and lunar phase (McGovern and McCarthy, 1992; Baras et al., 1998; Hedger et al., 2010). Lunar periodicity has been thought to influence the onset of the spawning migration of anguillid eels (Durif & Elie 2008). It has been shown that marine fish species show strong affinity to certain lunar phases (Henderson *et al.* 2014). However given the strong relationship between tidal currents and lunar phase it is hard to tease apart the true effect of the lunar cycle in these cases, unlike in lake environments. Interestingly in this study morph activity peaked on different lunar phases (Fig.6), significant increase in rate of movement for broad-headed individuals was observed on waxing lunar phases in contrast to highest activity on waning phases for narrow headed individuals. There is a paucity of data on yellow eel movement and the potential influence of lunar phases, Hedger et al. (2010) reported reduced areal ranges under high lunar illumination (full moon), but no effect was identified on absolute ground speed. Lamothe et al. (2000) identified homing during the new moon and Baras et al. (1998) & McGovern and McCarthy (1992) observed higher yellow eel activity under full moon events. The synchronicity in movement of eels in relation to lunar events is similar to that observed for marine species (Henderson et al., 2014). This study shows that there may be links between foraging activity and lunar periodicity in freshwater eels. For example the moonlight at the full moon is known to depress the activity of benthic invertebrates (e.g. Neveu & Echaubard, 1975) and thus may explain the rapid increase in narrow headed eel activity in the waxing lunar phases after full moon events. Temperature had a positive effect on average home rang size for both morphs and daily displacement of broad-headed eels but not narrow-headed individuals. The influence of temperature on eel movement has been noted by Hedger et al. (2010) who found that eels swam faster and covered larger areas when water was warm. Typically eels are more active at a higher water temperature (Tesch, 2003).

In conclusion, the present study indicates that the movement patterns of lake dwelling European eels are complex and can be influenced by foraging behaviour as well as predictable environmental factors. Further studies of yellow eel behaviour and habitat use should take into account behavioural differences and whether the relationship between morphology and spatial patterns is observed in other ecosystems. Given the urgent need to design effective surveys of population size and distribution of eels, the information provided from these data can aid in survey design and the implementation of effective conservation strategies for this endangered fish (Jacoby & Gollock 2014).

Acknowledgments

This work was supported by funding from the European Union’s INTERREG IVA Programme (project 2859 ‘IBIS’) managed by the Special EU programmes Body. The authors would like to thank John Boyle of the Lough Finn Angling Association and staff at the Loughs Agency for technical assistance. The authors would also like to thank IBIS students & staff who helped with field work and technical assistance.

Reference

Adams, C. E., Fraser, D., Huntingford, F. A., Greer, R. B., Askew, C. M., & A. F. Walker, 1998. Trophic polymorphism amongst arctic charr from Loch Rannoch, Scotland. Journal of Fish Biology 52: 1259-1271.

Araújo, M. S., Bolnick, D. I., Martinelli, L. A., Giaretta, A. A., & S. F. Dos Reis, 2009. Individual-level diet variation in four species of Brazilian frogs. Journal of Animal Ecology: 78: 848-856.

Baras, E., Jeandrain, D., Serouge, B. & J.C. Philippart, 1998. Seasonal variations of time and space utilisation by radio-tagged yellow eels *Anguilla anguilla* (L.) in a small stream. Hydrobiologia 371/372: 187-198.

Béguer-Pon, M., Castonguay, M., Benchetrit, J., Hatin, D., Legault, M., Verreault, G. & J. J. Dodson, 2015. Large-scale, seasonal habitat use and movements of yellow American eels in the St. Lawrence River revealed by acoustic telemetry. Ecology of Freshwater Fish 24: 99-111

Bell, A. M., 2007. Future directions in behavioural syndromes research. Proceedings of the Royal Society: Biological Sciences 274: 755-761.

Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Husley CD, & M.L. Forister, 2003. The ecology of individuals: incidence and implications of individual specialization. American Naturalist 161:1–28

Borger, L., B. D. Dalziel, and J. M. Fryxell 2008. Are there general mechanisms of animal home range behaviour? A review and prospects for future research. Ecology Letters 11:637–650

Bozeman, E. L., Helfman, G. S., & T. Richardson, 1985. Population size and home range of American eels in a Georgia tidal creek. Transactions of the American Fisheries Society 114:821-825.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24: 346-352.

Calcagno, V., & C. de Mazancourt, 2010. glmulti: an R package for easy automated model selection with (generalized) linear models. Journal of Statistical Software 34: 1-29.

Clark, C.W. & D.A. Levy, 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. American Naturalist 131: 271–290.

Cooke, S.J., Hinch, S., Lucas, M.C. & M. Lutcavage, 2012. Biotelemetry and biologging. In: Fisheries Techniques 3rd ed., (eds. A. Zale, D. Parrish & T. Sutton), pp. 819-881. American Fisheries Society, Bethesda, Maryland.

Cucherousset, J., Acou, A., Blanchet, S., Britton, J. R., Beaumont, W. R., & R. E. Gozlan, 2011. Fitness consequences of individual specialisation in resource use and trophic morphology in European eels. Oecologia 167: 75-84.

Dahlgren, C. P., & Eggleston, D. B. 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. Ecology, 81: 2227-2240.

Daverat, F., Limburg, K.E., Thibanlt, I., Shiao, J.C., Dodson, J.J., Caron, F., Tzeng, W.N., Iizuka, Y., & H. Wickstrom, 2006. Phenotypic plasticity of habitat use by three temperate eel species,*Anguilla anguilla*, *Anguilla japonica* and *Anguilla rostrata*. Marine Ecology Progress Series, 308: 231-241.

Durif, C. M. F., & P. Elie, 2008. Predicting downstream migration of silver eels in a large river catchment based on commercial fishery data. Fisheries Management and Ecology 15: 127-137.

Durif, C., Dufour, S. & P. Elie, 2005. The silvering process of *Anguilla anguilla*: a new classification from the yellow resident to the silver migrating stage. Journal of Fish Biology 66: 1025–1043.

Ford, T. E. & E. Mercer, 1986. Density, size distribution and home range of American eels, Anguilla rostrata, in a Massachusetts salt marsh. Enviromental Biology of Fishes 17: 309–314.

Fraley C, & A.E. Raftery, 2006. MCLUST version 3 for R: Normal mixture modelling and model-based clustering. Technical report no. 504. Department of statistics, University of Washington.

Fu, S. J., Zeng, L. Q., Li, X. M., Pang, X., Cao, Z. D., Peng, J. L., & Y. X. Wang, 2009. The behavioural, digestive and metabolic characteristics of fishes with different foraging strategies. Journal of Experimental Biology 212: 2296-2302.

Garduño-Paz, M. V., & C. E. Adams, 2010. Discrete prey availability promotes foraging segregation and early divergence in Arctic charr, *Salvelinus alpinus*. Hydrobiologia 650: 15-26.

Geospatial Modelling Environment (Version 0.7.2.1). (software). URL: http://www.spatialecology.com/gme.

Hedger, R. D., Dodson, J. J., Hatin, D., Caron, F., & D. Fournier, 2010. River and estuary movements of yellow-stage American eels *Anguilla rostrata*, using a hydrophone array. Journal of Fish Biology 76:1294-1311.

Hedger, R. D., Martin, F., Dodson, J. J., Hatin, D., Caron, F., & F. G. Whoriskey, 2008. The optimized interpolation of fish positions and speeds in an array of fixed acoustic receivers. ICES Journal of Marine Science 65:1248-1259.

Helfman, G. S., Stoneburner, D. L., Bozeman, E. L., Christian, P. A. & R .Whalen, 1983. Ultrasonic telemetry of American eel movements in a tidal creek. Transactions of the American Fisheries Society 112: 105–110.

Henderson, M. J., Fabrizio, M. C., & J. A. Lucy, 2014. Movement patterns of summer flounder near an artificial reef: Effects of fish size and environmental cues. Fisheries Research 153: 1-8.

Hodder, K., J. Masters, W. Beaumont, R. Gozlan, A. Pinder, C. Knight, & R. Kenward. 2007. Techniques for evaluating the spatial behaviour of river fish. Hydrobiologia 582:257-269

Ide, C., De Schepper, N., Christiaens, J., Van Liefferinge, C., Herrel, A., Goemans, G. & D. Adriaens. 2011. Bimodality in head shape in European eel. Journal of Zoology 285: 230-238.

Jackson, D. A., Peres-Neto, P. R. & J. D. Olden. 2001. What controls who is where in freshwater fish communities the roles of biotic, abiotic, and spatial factors. Canadian Journal of Fisheries and Aquatic Sciences 58:157-170.

Jacoby, D. & Gollock, M. (2014). *Anguilla anguilla*. In: IUCN 2014. IUCN Red List of Threatened Species. Version 2012.1. http://www.iucnredlist.org/details/60344/0 (last accessed on 05 August 2015)

Jetz, W., Carbone, C., Fulford, J., & J. H. Brown, 2004. The scaling of animal space use. *Science* 306:266-268.

Kass, R. E., & A. E. Raftery. 1995. Bayes factors. Journal of the American Statistical Association 90: 773-795.

Killen, S. S., Costa, I., Brown, J. A., & Gamperl, & A. K. 2007. Little left in the tank: metabolic scaling in marine teleosts and its implications for aerobic scope. Proceedings of the Royal Society B: Biological Sciences 274: 431-438.

Kobler, A., Klefoth, T., Mehner, T., & R. Arlinghaus 2009. Coexistence of behavioural types in an aquatic top predator: a response to resource limitation? Oecologia 161: 837-847.

Kramer, D. L., & M. R. Chapman, 1999. Implications of fish home range size and relocation for marine reserve function. Environmental biology of Fishes 55: 65-79.

Kristjansson, B. K., Skulason, S., & D. L. Noakes, 2002. Morphological segregation of Icelandic threespine stickleback (Gasterosteus aculeatus L).Biological Journal of the Linnean Society 76: 247-257.

Laffaille, P., Baisez, A., Rigaud, C., & E. Feunteun, 2004. Habitat preferences of different European eel size classes in a reclaimed marsh: a contribution to species and ecosystem conservation. Wetlands 24: 642-651.

Lammens, E. H., & J. T. Visser, 1989. Variability of mouth width in European eel, *Anguilla anguilla*, in relation to varying feeding conditions in three Dutch lakes. Environmental Biology of Fishes 26: 63-75.

Lamothe, P. J., Gallagher, M., Chivers, D. P., & J. R. Moring, 2000. Homing and movement of yellow-phase American eels in freshwater ponds. Environmental Biology of Fishes 58: 393-399.

Lucas, M. C. & E. Baras, 2000. Methods for studying spatial behaviour of freshwater fishes in the natural environment. Fish and Fisheries 1: 283–316.

Marshell, A., Mills, J. S., Rhodes, K. L., & J. McIlwain, 2011. Passive acoustic telemetry reveals highly variable home range and movement patterns among unicornfish within a marine reserve. Coral Reefs 30: 631-642.

McGovern, P. & T. K. McCarthy, 1992. Local movements of freshwater eels (Anguilla anguilla L.) in western Ireland. In I. G. Priede & S. M. Swift (eds), Wildlife Telemetry: Remote Sensing and Monitoring of Animals. Ellis Horwood, Chichester, UK: 319–327.

Mitchell, M. S., and R. A. Powell 2004. A mechanistic home range model for optimal use of spatially distributed resources. Ecological Modelling 177:209–232.

Moriarty, C., & W. Dekker, 1997. *Management of the European eel*. Marine Institute.

Morrison, W. E., & D. H. Secor, 2003. Demographic attributes of yellow-phase American eels (*Anguilla rostrata*) in the Hudson River estuary. Canadian Journal of Fisheries and Aquatic Sciences 60: 1487-1501.

Neveu, A. &M. Echaubard, 1975. La dérive estivale des invertébrés aquatiques et terrestres dans un ruisseau du Massif Central: la Couze Pavin. Ann. Hydrobioliga 6: 1–26.

Parker, S. J. 1995. Homing ability and home range of yellow-phase American eels in a tidally dominated estuary. Journal of the Marine Biological Association of the United Kingdom 75: 127-140.

Pearce, F., Carbone, C., Cowlishaw, G., & N. J. Isaac, 2013. Space-use scaling and home range overlap in primates. Proceedings of the Royal Society B: Biological Sciences 280:201- 222.

Peters, R.H. 1986. The ecological implications of body size. New York: Cambridge University Press.

Pinheiro, J.C. & D.M. Bates, 2000. Mixed effects models in S and S-PLUS. New York, NY: Springer.

Powell, R. A. 2000. Animal home ranges and territories and home range estimators. Pp. 65–110 in Research techniques in animal ecology: controversies and consequences (L. Boitani and T. K. Fuller, eds.). Columbia University Press, New York.

Powell, R. A., & M. S Mitchell, 2012. What is a home range? Journal of Mammalogy 93:948-958.

Proman, J. M., & J. D. Reynolds, 2000. Differences in head shape of the European eel, *Anguilla anguilla* (L.). Fisheries Management and Ecology 7: 349-354.

Pyke, G. H. (1984). Optimal foraging theory: a critical review. Annual Review of Ecology and Systematics, 523-575.

R Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

Riley, W. D., Walker, A. M., Bendall, B., & M. J. Ives, 2011. Movements of the European eel (*Anguilla anguilla*) in a chalk stream. Ecology of Freshwater Fish 20:628-635.

Rosten, C.M., Gozlan, R.E., & M.C. Lucas, 2013. Diel and seasonal movements of the critically endangered eel. Vann 1: 89-95.

Schulze, T., Kahl, U., Radke, R. J. & J. Benndorf, 2004. Consumption, abundance and habitat use of *Anguilla anguilla* in a mesotrophic reservoir. Journal of Fish Biology 65:1543–1562.

Simpfendorfer, C. A., Heupel, M. R., & R. E. Hueter, 2002. Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. Canadian Journal of Fisheries and Aquatic Sciences 59: 23-32.

Siwertsson, A., Knudsen, R., Præbel, K., Adams, C. E., Newton, J., & P. A. Amundsen, 2013. Discrete foraging niches promote ecological, phenotypic, and genetic divergence in sympatric whitefish (*Coregonus lavaretus*). Evolutionary Ecology 27: 547-564.

Skulason, S., & T. B. Smith, 1995. Resource polymorphisms in vertebrates. Trends in ecology & evolution 10:366-370.

Swihart, R. K., Slade, N. A., & B. J. Bergstrom, 1988. Relating body size to the rate of home range use in mammals. Ecology 393-399.

Tesch, F. W., 1967. Homing of eels (*Anguilla anguilla*) in the southern North Sea. Marine Biology 1: 2-9.

Tesch, F. W., 2003. The Eel. Oxford: Blackwell Publishing.

Thorstad, E. B., Økland, F., Westerberg, H., Aarestrup, K., & J. D. Metcalfe, 2013. Evaluation of surgical implantation of electronic tags in European eel and effects of different suture materials. Marine and Freshwater Research 64: 324-331.

Thibault, I., Dodson, J. J., & Caron, F. (2007). Yellow-stage American eel movements determined by microtagging and acoustic telemetry in the St Jean River watershed, Gaspé, Quebec, Canada. Journal of Fish Biology 71: 1095-1112.

Villegas-Ríos, D., Alós, J., March, D., Palmer, M., Mucientes, G., & F. Saborido-Rey, 2013. Home range and diel behavior of the ballan wrasse, *Labrus bergylta*, determined by acoustic telemetry. Journal of Sea Research 80:61-71.

Walker, A. M., Godard, M. J., & P. Davison, 2014. The home range and behaviour of yellow-stage European eel *Anguilla anguilla* in an estuarine environment. Aquatic Conservation: Marine and Freshwater Ecosystems 24: 155-165.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70: 164-168.

Yokouchi, K., Aoyama, J., Miller, M. J., McCarthy, T. K., & K. Tsukamoto, 2009. Depth distribution and biological characteristics of the European eel *Anguilla anguilla* in Lough Ennell, Ireland. Journal of Fish Biology 74:857-871.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & G.M Smith, 2009. Mixed effects models and extensions in ecology with R. New York, NY: Springer.

Electronic reference

NOAA, 2014: www.srrb.noaa.gov/highlights/sunrise/calcdetails.html (last acessed 1-4-2015)

Lazaridis, E. 2015: “Lunar” package R: http://cran.rproject.org/web/packages/lunar/lunar.pdf (last acessed 1-4-2015)

FIGURE 1. Lough Finn and river finn outflow stream, receiver positons (black dots) and omnidirectional detection range from acoustic listening station (black circles).

FIGURE 2 Landmark placement for digitizing head shape. 1) most anterior point of the snout; 2) left rostral nostril; 3) right rostral nostril; 4) outermost jaw in line with rostral border of eye; 5) rostral border of eye (left); 6) outermost jaw in line with rostral border of eye (right); 6) rostral border of eye right; 8) caudal border of eye (left); 9) caudal border of eye right.

FIGURE 3. Relationship between home range size (KUD_{95}) and length of individuals (log transformed), broad heads black circles and associated trend line solid black line and narrow heads hollow circles and associated trend line dashed line

FIGURE 4: The average displacement rate (BLh^{-1}) per hour (facet by month) for broad (B=grey line) and narrow-headed (N=black line) individuals. Crepuscular periods are represented by light shading (range = min and max sunrise/sunset for each month, NOAA 2014).

FIGURE 5: The average hourly displacement rates (BLh^{-1}) for broad-headed (white box) and narrow-headed (grey box) individuals in different light categories. B = Broad-headed N= Narrow-headed

FIGURE 6 Average daily displacement (BLh^{-1}) of tagged individuals grouped by morph type during lunar phases. Error bars ± 1 standard error.

Fig 1.

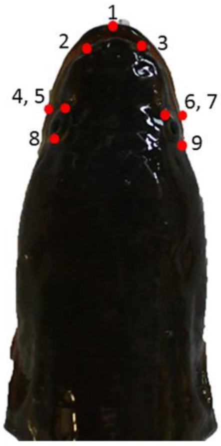

Fig 2.

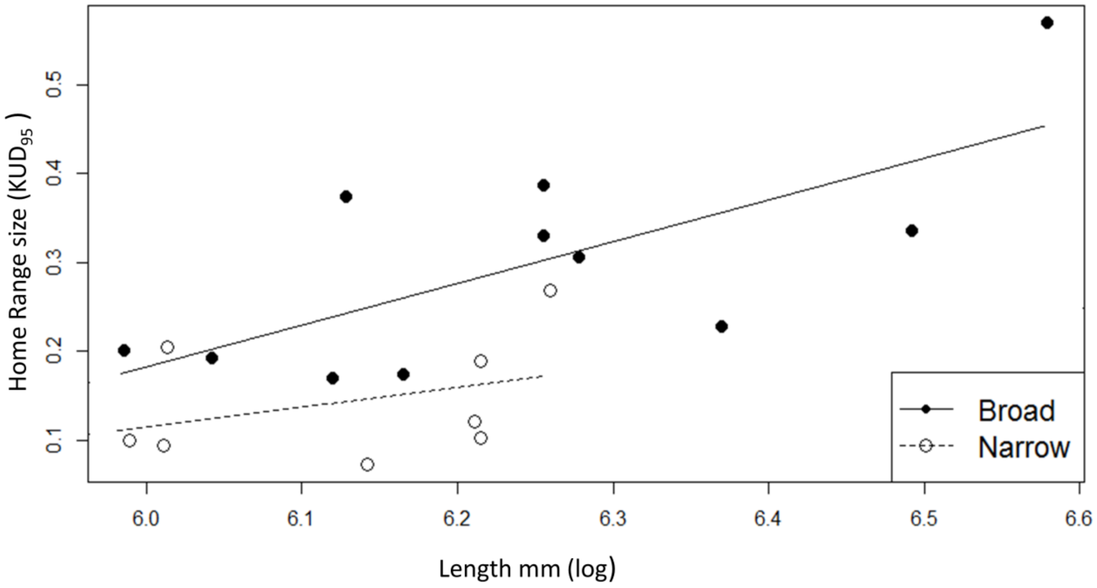
Home Range size (KUD$_{95}$)
0.1
0.2
0.3
0.4
0.5
6.0
6.1
6.2
6.3
6.4
6.5
6.6
Length mm (log)
Broad
Narrow

Fig 3.

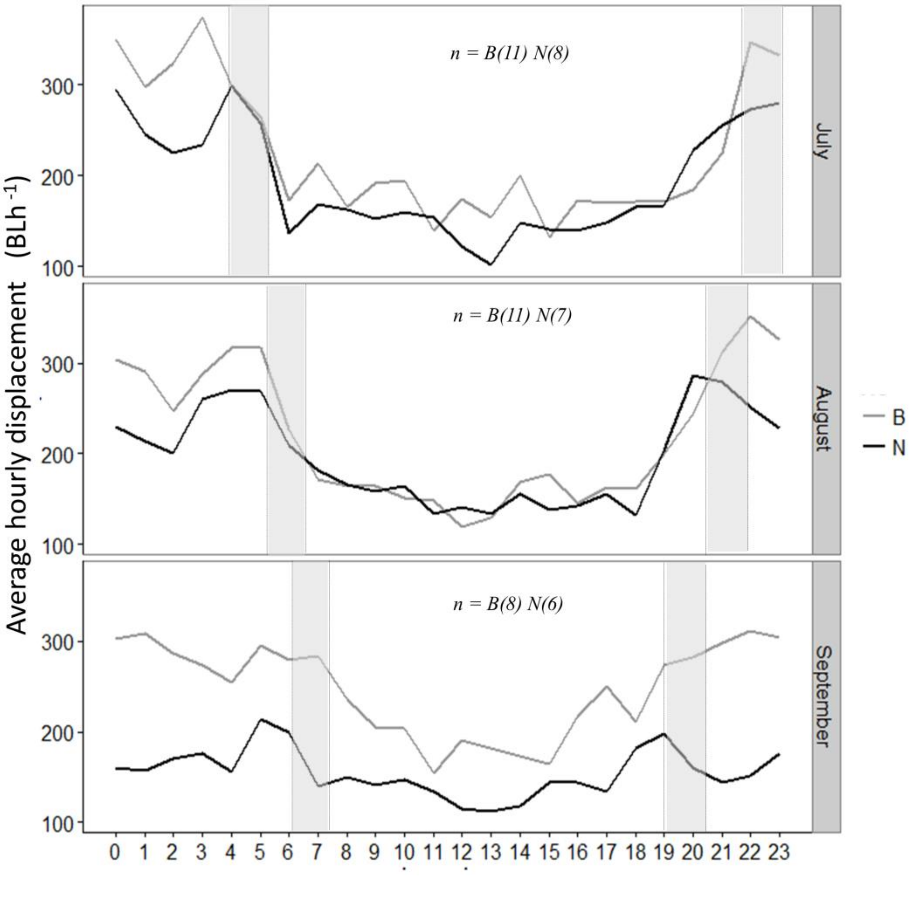
n = B(11) N(8)
n = B(11) N(7)
n = B(8) N(6)
July
August
September
Average hourly displacement (BLh-1)
100
200
300
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23
B
N

Fig 4

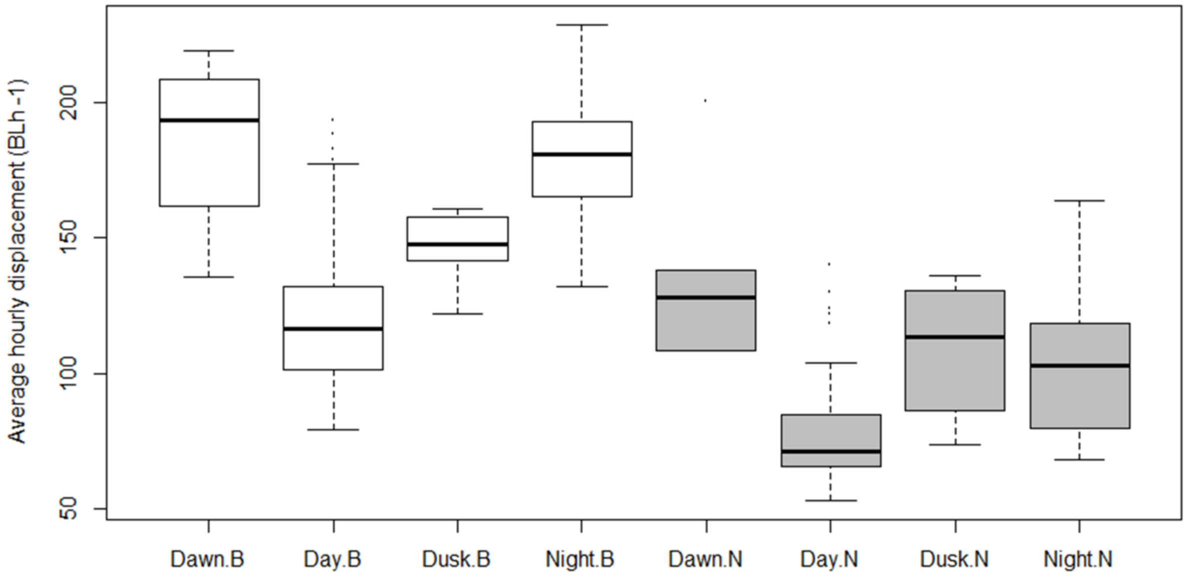
Average hourly displacement (BLh -1)
50
100
150
200
Dawn.B
Day.B
Dusk.B
Night.B
Dawn.N
Day.N
Dusk.N
Night.N

Fig 5.

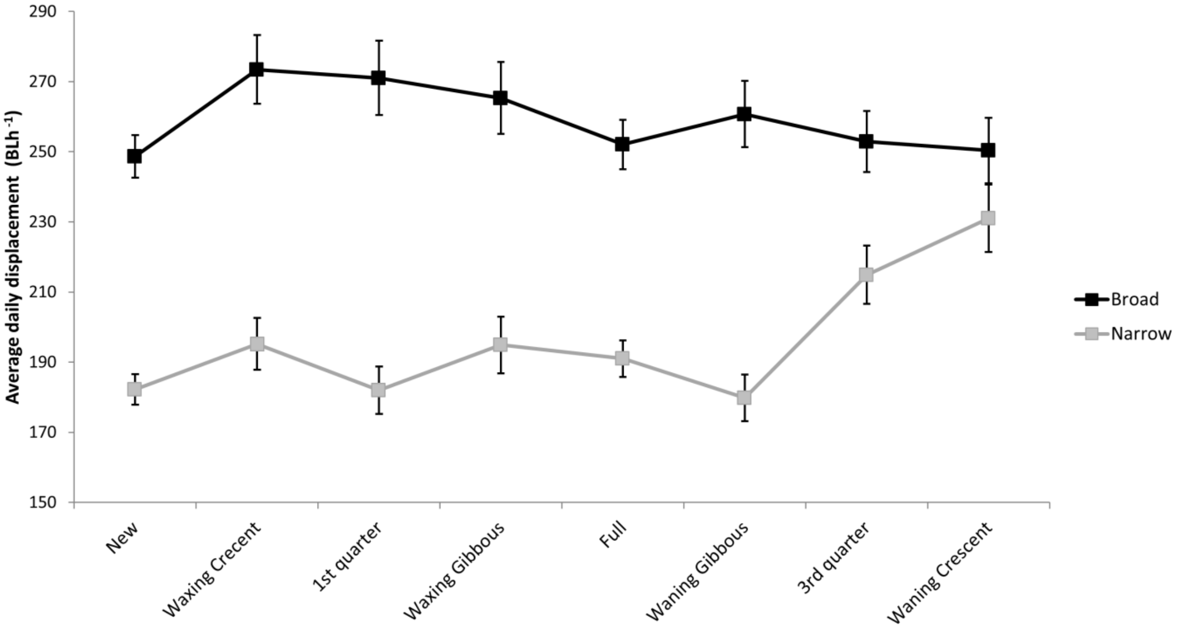

Fig 6

Table 1. Characteristics of the 20 individuals tagged and detection span. B=broad-headed, N=narrow-headed._2318_* excluded from analysis

Fish ID	Release Date	TL (mm)	Weight (g)	Detection Span (days)	MCLUST group	Morphotype	HW:TL
_2318_*	02/07/2013	390	90	26	1	B	0.038
2327	02/07/2013	398	101	91	1	B	0.048
2315	02/07/2013	421	117	53	1	B	0.036
2329	02/07/2013	455	154	59	1	B	0.044
2323	27/06/2013	459	154	95	1	B	0.048
2320	02/07/2013	476	160	91	1	B	0.040

2325	27/06/2013	521	320	95	1	B	0.047
2340	02/07/2013	521	306	91	1	B	0.046
2337	27/06/2013	533	243	95	1	B	0.043
2326	02/07/2013	584	371	90	1	B	0.050
2332	02/07/2013	660	540	91	1	B	0.048
2335	02/07/2013	720	602	44	1	B	0.046
2333	27/06/2013	399	130	91	2	N	0.028
2339	02/07/2013	408	102	91	2	N	0.025
2302	02/07/2013	409	94	90	2	N	0.022
2303	27/06/2013	465	218	95	2	N	0.026
2322	27/06/2013	498	201	95	2	N	0.029
2330	02/07/2013	500	214	91	2	N	0.032
2336	02/07/2013	500	224	90	2	N	0.024
2334	02/07/2013	523	216	52	2	N	0.027

Table 2: Mean Kernel Utilisation Distribution 95 and Kernel Utilisation Distribution 50 per month and overall mean for the duration of tagging period.

Month	Broad KUD_{50}	Broad KUD_{95}	Narrow KUD_{50}	Narrow KUD_{95}
July	0.066	0.341	0.031	0.179
August	0.113	0.251	0.022	0.112
September	0.048	0.292	0.017	0.103
Overall mean (S.E)	0.076 (0.012)	0.295 (0.016)	0.023(0.003)	0.131(0.16)

Table 3: Temporal stability denoted by percentage home range overlap for home range Mean Kernel Utilisation Distribution 95 and core range Kernel Utilisation Distribution 50 between months over the study period. (Refer to text for statistical analysis). B= broad-headed and N= narrow-headed.

I.D	TL	Morphotype	KUD_{50} (Jul-Aug)	KUD_{50} (Aug-Sep)	Mean monthly KUD_{50} overlap (50%)	KUD_{95} (Jul-Aug)	KUD_{95} (Aug-Sep)	Mean monthly KUD_{95} overlap (95%)
2315	421	B	62	-	62	62	-	62
2320	476	B	73	72	72.5	74	85	79.5
2323	459	B	29	49	39	36	53	44.5
2325	521	B	6	86	46	61	89	75
2326	584	B	29	64	46.5	73	86	79.5
2327	398	B	32	32	32	58	78	68
2329	455	B	64	-	64	74	-	74
2332	660	B	62	79	70.5	81	63	72
2335	720	B	28	-	28	59	-	59
2337	533	B	66	56	61	87	59	73
2340	521	B	50	76	63	75	86	80.5
2302	409	N	37	52	44.5	60	65	62.5
2303	465	N	52	68	60	88	71	79.5
2322	498	N	26	-	26	79	-	79
2330	500	N	0	19	9.5	54	61	57.5
2333	399	N	21	52	36.5	74	69	71.5
2334	523	N	10	-	10	65	-	65
2336	500	N	0	0	0	90	49	69.5
2339	408	N	61	58	59.5	84	80	82

Supplementary Tables

Table S1: Fish locations (n=108) stratified proportionally in each time of day category over the three month study period. The number (*n*) of individual eels from each morph; Broad or Narrow for which home range was calculated for each month.

Month	Dawn	Day	Dusk	Night	Broad (*n*)	Narrow (*n*)
July	4	66	5	33	*11*	*8*
August	3	61	3	41	*11*	*7*
September	3	52	3	50	*8*	*6*

Table S2: . Summary of spatial utilisation information for *A.anguilla*. KUD_{95}= kernel utilisation distribution based on 95% of the positions (home range km^2); KUD_{50}= kernel utilisation distribution based on 50% of the positions (core area km2). B= broad-headed and N= narrow-headed.

Code	Jul50	Jul95	Aug50	Aug95	Sep50	Sep95	Morph
2315	0.026	0.219	0.017	0.164	-	-	B
2320	0.058	0.164	0.032	0.165	0.035	0.193	B
2323	0.227	0.816	0.028	0.186	0.017	0.119	B
2325	0.079	0.520	0.067	0.315	0.065	0.325	B
2326	0.008	0.196	0.002	0.234	0.012	0.238	B
2327	0.053	0.251	0.008	0.166	0.064	0.185	B
2329	0.025	0.164	0.023	0.174	-	-	B
2332	0.068	0.400	0.057	0.228	0.045	0.377	B
2335	0.099	0.556	0.914	0.582	-	-	B
2337	0.032	0.214	0.027	0.186	0.079	0.517	B
2340	0.052	0.250	0.072	0.355	0.070	0.383	B
Mean(S.E)	*0.066 (0.02)*	*0.341 (0.06)*	*0.113(0.08)*	*0.251(0.03)*	*0.048(0.01)*	*0.292(0.04)*	
2302	0.065	0.369	0.027	0.157	0.020	0.086	N
2303	0.024	0.130	0.031	0.152	0.017	0.082	N
2322	0.001	0.088	0.002	0.058	-	-	N
2330	0.022	0.171	0.021	0.132	0.001	0.003	N
2333	0.027	0.122	0.030	0.090	0.018	0.087	N
2334	0.047	0.268	-	-	-	-	N
2336	0.033	0.186	0.025	0.106	0.035	0.274	N
2339	0.033	0.103	0.018	0.090	0.011	0.087	N
Mean(S.E)	*0.031(0.001)*	*0.179(0.03)*	*0.022(0.003)*	*0.112(0.01)*	*0.017(0.004)*	*0.103 (0.03)*	